THE GENERA OF ELATINACEAE IN THE SOUTHEASTERN UNITED STATES¹

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ELATINACEAE Dumortier, Anal. Fam. Pl. 44, 49. 1829, "Elatinideae," nom. cons.

(WATERWORT FAMILY)

Annual or perennial plants (up to 50 cm tall) of aquatic or moist terrestrial habitats. Roots fibrous; lower nodes usually with adventitious roots. Plants glabrous or glandular pubescent throughout, with unicellular or multicellular multiseriate capitate trichomes. Leaves opposite or decussate, entire or coarsely serrate; stomata anomocytic; stipules scarious. Flowers small, actinomorphic,

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Tetracytic, according to Cronquist and Metcalfe & Chalk. Microscopic examination of leaves from each of the following collections revealed in all cases an anomocytic arrangement (4–8 irregularly shaped subsidiary cells around the guard cells). Elatine Alsinastrum L.—U.S.S.R., Octjabreva et al. 5880 (A); E. americana (Pursh) Arnott—Connecticut, Bridgeport, Eames s.n., 6 Aug. 1899 (GH); E. minima (Nutt.) Fischer & Meyer—Connecticut, Lyme, Tucker & Linke 3176 (NYS), and Stonington, G. C. & J. R. Tucker 3217 (NYS); E. triandra Schkuhr—Wyoming, Lincoln Co., Payson & Armstrong 3434 (GH). Bergia texana (Hooker) Seub.—Louisiana, Red River Parish, SW of Crichton, Thieret 20618 (LAF), and Grant Parish, SW of Montgomery, Thieret 24749 (LAF).

© President and Fellows of Harvard College, 1986. Journal of the Arnold Arboretum 67: 471–483. October, 1986. hypogynous, borne singly or in small clusters in the axils of leaves. Sepals 2–5 [or 6], free or barely united basally. Petals membranaceous, 2–5, free. Stamens [2 or] 3–6[–10], in 1 or 2 whorls, the outer whorl alternate with the petals; anthers broadly ovoid, dehiscing by longitudinal slits; pollen prolate to subspheroidal, tricolporate, 2- or 3-nucleate when shed. Ovary [2 or] 3–5-locular, ovoid to depressed ovoid; placentation axile or basal, the partitions not reaching the summit of the ovary in some species of *Bergia*; ovules numerous, anatropous, bitegmic, tenuinucellar; megagametophyte (embryo sac) of the Polygonum type. Fruit a thin-walled septifragal capsule. Seeds ellipsoid to oblong, 0.5–1.5 mm long, with finely reticulate [smooth] surfaces; endosperm very little or none; embryo straight, filling nearly the entire seed; germination epigeal. Base chromosome numbers 6, 9. Type Genus: *Elatine* Linnaeus.

A small, nearly cosmopolitan family of two genera, *Bergia* L. and *Elatine*, and about 35 species. Both genera are represented in the United States. One species of *Bergia* and two of *Elatine* occur in the Southeast.

The Elatinaceae are herbaceous or suffrutescent aquatic or wetland plants with opposite [whorled] simple [tripartite or quadripartite] leaves with paired interpetiolar stipules. The inconspicuous two- to five- [or six-]merous actinomorphic flowers are borne singly or in dichasia in the upper leaf axils. The small, thin-walled capsular fruits are septifragal, and the seed coats are characteristically strongly sculptured.

Adanson noted a similarity between *Elatine* and the Caryophyllaceae in their opposite leaves, small flowers, and tiny seeds. This view was also held by De Jussieu, De Candolle, Bentham & Hooker, Bessey, and Hutchinson. As early as 1827, however, Cambessèdes noted similarities between the Elatinaceae and the Guttiferae (*sensu lato*, including the Hypericaceae). Gray, in his discussion of the taxonomy of the family, emphasized its similarities to the Guttiferae. Niedenzu, and later Melchior in succeeding editions of Engler's *Syllabus*, placed the family in the Parietales. Cronquist, Takhtajan, and Thorne concurred in the placement of the Elatinaceae in the Theales and agreed that its affinities lie with the Guttiferae (Clusiaceae). Corner noted a similarity in the structure of the seeds of the two families. The sculpturing of the seed coat in the Elatinaceae is very much like that of Guttiferae subfam. Bonnettioideae, particularly the genus *Ploiarium* Korth.

The wood anatomy of *Bergia suffruticosa* Fenzl indicates that the most likely relationship of the family is with the Guttiferae (Carlquist). The following similarities are apparent: occurrence of simple perforation plates, presence of vasicentric tracheids and fibriform vessel elements, predominance of uniseriate rays, vertical orientation of scalariform vessel—ray pitting, absence of intraxylary phloem, presence of brownish compounds [tannins?] in the parenchyma, and occurrence of druses and solitary crystals.

Melikian & Dildarian, on the basis of anatomical and palynological studies, and Walia & Kapil, on the basis of embryological studies of the Frankeniaceae, a family usually placed in the Parietales, concluded that the Elatinaceae and the Frankeniaceae are closely related. However, because several of the similarities they listed (e.g., trinucleate pollen, bitegmic ovules, and monosporic

embryo sacs) characterize many families of angiosperms, a close relationship between the Frankeniaceae and Elatinaceae seems doubtful.

The family is little known chemically (Gibbs, Hegnauer). Several phenolic acids (delphinidin, ellagic acid, quercetin, cyanidin, kaempferol) have been reported from Bergia (species not indicated); saponins and alkaloids are absent from Bergia, while tannins occur in at least two species. Bergia suffruticosa has been found to lack alkaloids. Elatine appears to be poor in taxonomically interesting chemicals: E. gratioloides A. Cunn. contains no alkaloids, saponins, or leucoanthocyanins; E. hexandra (Lapierre) DC. contains ellagic acid but lacks other phenolic compounds. The petals of E. americana (Fernald) and E. minima (pers. obs.) are sometimes pinkish, probably because of anthocyanins. Gibbs reported druses and raphides to be absent in the family, while Metcalfe & Chalk noted the occurrence of cluster crystals in the endodermis and pith of Bergia (species not indicated), and Carlquist recorded druses and solitary crystals in the parenchyma of B. suffruticosa.

The family is of little economic importance. No species is recorded as being gathered for use as food or condiments, nor is any reported to be poisonous to humans or livestock. Bergia suffruticosa, 2n = 36, is employed in Pakistan in folk medicine and in Sudan as a poultice for broken bones.

Several species of Bergia are weeds in rice fields in the Old World, as are species of Elatine in California, Japan, and Java. The seeds and foliage of Elatine are eaten by ducks, and the plants are considered to be beneficial because they consolidate mud and provide cover for small fish. Several species (e.g., E. Hydropiper L. and E. triandra) are cultivated as "turf-forming" foliage plants in aquaria. They are reported to be easy to propagate from either cuttings or seed.

The family is poorly known taxonomically. A comprehensive worldwide revisionary study of Bergia has never been made. The only global monograph of Elatine appeared in the 1870's (Dumortier). Niedenzu's account of the Elatinaceae in Die Natürlichen Pflanzenfamilien is of limited use for the identification of specimens because of its synoptic nature. Most taxonomic investigation in this family has either involved floristics or been concerned chiefly with the description of new taxa. Most workers seem to have been familiar only with the species represented in their herbaria.

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KEY TO THE GENERA OF ELATINACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: small, soft, herbaceous or woody-based annual or subperennial plants growing in or near water; glabrous or glandular pubescent throughout; leaves

opposite, decussate, stipules scarious; flowers inconspicuous, borne singly or in small axillary clusters; sepals and petals 3–5; ovaries globose to ovoid; styles very short; capsules septifragal; seeds small, more or less reticulate.

1. Bergia Linnaeus, Mant. Pl. 2: 152. 1771.

Annual [or perennial], herbaceous [or suffrutescent], simple to much-branched procumbent to ascendent plants of moist, disturbed soils; often occurring on sand bars along rivers. Roots fibrous, much branched from a conspicuous taproot; adventitious roots usually formed in the axils of the lower leaves. Stems herbaceous but woody and thickened at base, glandular pubescent throughout. Leaves decussate, glandular pubescent on both surfaces [or glabrous], the margins serrate; stipules scarious, glandular pubescent. Flowers solitary or in dichasia in the axils of the leaves. Sepals 5, free, acute, mucronate, with a thickened midvein and scarious margins, glandular pubescent throughout. Petals 5, oblong, membranaceous, glabrous, whitish. Stamens 5 [or 10]; anthers ellipsoid; pollen tricolpate, subprolate to spheroidal, sexine reticulate to reticulate-polybrochate, binucleate when shed. Ovary ovoid, 5 [or 6]-locular [the partitions not reaching the summit in some Asian species], each locule with numerous ovules; stigmas 5; styles 5, very short. Seeds oblong, slightly curved, brown, obscurely reticulate [smooth]. Base chromosome number 6. Type species: B. capensis L. (Named for Peter Jonas Bergius, 1730-1790, Swedish botanist and student of Linnaeus.)

A genus of about 25 species, primarily of the Old World tropics. Three species occur in the New World: Bergia arenarioides Camb. in Brazil; B. capensis, 2n = 18, native to Africa and southern Asia, collected as an adventive on the Pacific coast of South America (Molau); and B. texana (Hooker) Seub., ranging from Illinois, Missouri, Arkansas (Desha County), and Louisiana (Bossier, Red River, St. Mary, and Grant parishes), westward to northern Mexico, southern California, and eastern Washington.

The center of greatest diversity in the genus is in eastern and southern Africa, where some 20 species occur. By contrast, there are only five species in southern Asia and two in Malesia and Australia. *Bergia capensis*, which ranges from southern Africa to India and Indonesia, is the most widely distributed species in the genus. It is also recorded as an adventive weed in rice fields in Spain and Portugal.

Niedenzu divided the genus into two sections. He placed *Bergia texana* in sect. Bergia (sect. *Dichasianthae* Niedz.), in which the flowers are borne in axillary dichasia. Species of sect. Monanthae Niedz. are characterized by solitary axillary flowers.

Apparently nothing is known about the pollination biology of any species of *Bergia*.

About half the species of Bergia are aquatic; the remainder are plants of

moist soils. According to D'Almeida, *B. capensis* has dimorphic roots. The plumose water roots lack root hairs but frequently have chloroplasts in the cortex and thus supplement the leaves as assimilatory organs. The stout whitish roots that anchor the plant in the muddy bottom of the pond or pool bear very few lateral roots but are almost completely covered by root hairs.

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2. Elatine Linnaeus, Sp. Pl. 1: 367. 1753; Gen. Pl. ed. 5. 172. 1754.

Small, aquatic or emergent, herbaceous annuals or short-lived perennials of marshes, streambanks, shores of lakes and ponds, mud flats, pools, ditches, and rice fields. Roots slender, soft, the exposed portions sometimes with chloroplasts in the cortical cells. Stems soft, chlorophyllous, with 5–11 air chambers visible in cross section; stems upright when growing underwater, more or less procumbent when growing on wet soil or mud. Leaves opposite, sessile or with short petioles, blades narrowly to broadly elliptic to nearly orbiculate, one-fourth to three-fourths as long as wide, entire or essentially so (with hydathodes on the margins at the ends of the veins), the apices rounded, the bases cuneate to somewhat rounded. Flowers solitary in the axils of the upper leaves, [2 or]

3 [or 4]-merous. Sepals membranaceous, very pale green, inconspicuous. Petals the same number as sepals, membranaceous, pale greenish white, about as long as the sepals [small floral nectaries present in some species]. Stamens [2 or] 3[-8]; filaments about half as long as to equaling the petals; anthers tetrasporangiate (sometimes bi- or trisporangiate in cleistogamous flowers), broadly ovoid, the connective apex subacute, prolonged slightly beyond the anther locules; pollen tricolporate, spheroidal to subprolate, sexine granulate to reticulate, trinucleate when shed. Ovaries broadly ovoid, [2 or] 3 [or 4]-locular, the partitions thin, fragile; placentation basal [axile]; styles 3; stigmas terminal, appressed to the ovary. Capsules subglobose or depressed ovoid, the walls thin, membranaceous, delicate, the seeds more or less visible within. Seeds cylindrical, straight or slightly curved, narrowly to broadly ellipsoid, the surface brown to yellowish brown, reticulate with a network of fine ridges forming hexagons [ovals]. Base chromosome number 9. Lectotype species: E. Hydropiper L.; see Britton & Brown, Illus. Fl. No. U. S. & Canada. ed. 2. 2: 538. 1913; also see Hitchcock & Green. (Elatine, a Greek plant name employed by Dioscorides and Tournefort and adopted by Linnaeus [Crit. Bot. 103. 1737; Philos. Bot. 144, 174. 1751]; also see Dumortier, Gray.)—WATERWORT, PIGMY MUDWORT.

A genus of about 25 species, interruptedly cosmopolitan in distribution, with species occurring on all continents except Antarctica. Ten species are native to North America and about 12 to Eurasia. There are five to seven species in South America, mostly in temperate and Andean regions. Three primarily European species occur in North Africa; none apparently grows in the central part of the continent, while two are reported from Zimbabwe and Namibia (Riley). Two species occur in India and Malesia; one, *Elatine gratioloides* Bentham, is found in Australia, New Zealand, and Fiji.

Two subgenera and three sections were named by Seubert, whose classification was followed by Niedenzu in *Die Natürlichen Pflanzenfamilien*. Subgenus Potamopitys (Adanson) Seub., containing only *Elatine Alsinastrum* of Europe and North Africa, is characterized by having whorled leaves. The remaining species, all of which have opposite leaves, comprise subg. Elatine (subg. *Hydropiper Moesz*). Subgenus Elatine contains two sections. Section Elatine (sect. *Elatinella Seub.*), in which the flowers have six to eight stamens in two whorls, includes about eight species of Eurasia, California (*E. heterandra*), and South America (*E. ecuadoriensis*). The remaining species, which have two or three stamens in one whorl, comprise sect. Crypta (Nutt.) Seub. and occupy nearly the total range of the genus. All North American species (except *E. heterandra*, q.v.) are included in this section. *Elatine heterandra* may have either three or six stamens per flower (Mason), thus shedding doubt on the reliability of stamen number in classification.

Two species occur in the Southeast.4 Elatine americana is known from col-

⁴The taxonomy used here follows Fernald (1917, 1941). An examination of numerous herbarium specimens (at A, CCNL, GA, GH, LAF, NEBC, and NYS) shows that *Elatine brachysperma* and *E. americana* are distinguishable on the basis of seed shape and pitting. Fassett (and Gleason) treated these species as varieties of the primarily Eurasian *E. triandra*.

lections in Jackson Co., North Carolina, and Vermillion Parish, Louisiana. It ranges northward to Newfoundland and southeastern Manitoba. It is also common in Australia and New Zealand (Moore & Betche, Cheeseman, Good). More recently, Aston treated these Southern Hemisphere populations as a species, *E. gratioloides*, but her description and illustration seem indistinguishable from those of *E. americana*.

The other southeastern species, *Elatine brachysperma*, occurs from Georgia westward to California. Specimens have been seen from Georgia (Hancock and Oglethorpe counties), Alabama (Perry County), and Louisiana (Cameron and Lafayette parishes).

Two additional species occur in northeastern North America. *Elatine minima* has a wide range, from Labrador to the Northwest Territories, southward to Virginia and Illinois. *Elatine triandra*, a Eurasian and western North American species, has been collected in Skowhegan, Maine, and Brooklyn, New York; in both localities it is believed to be an introduction from Europe. Five species—two endemic to California—occur in western North America.

Plants of *Elatine* grow as submersed or emergent plants in shallow fresh [brackish or alkaline] pools, lakes, ponds, and ditches. They often occur in artificial ponds that are seasonally drained or in natural pools that dry out. Many species show some adaptation to fluctuating water levels in having plants with different growth forms under water and on land. The most striking example of this dimorphism occurs in the European *E. Alsinastrum*, the only species with whorled leaves. The upper, emergent portion of the stem bears whorls of leaves with ovate blades 1–2 cm long, while the submersed lower stem has leaves divided into four capillary segments, thus giving the appearance of 12 leaves per node. In the remaining species terrestrial and aquatic forms are less different. In *E. americana* and *E. brachysperma* submersed plants have longer internodes and longer, narrower leaf blades and are darker green than littoral plants (Bicknell, Sculthorpe; illustrations in Fassett and Kupper & Gams).

Knowledge of the pollination biology of *Elatine* is incomplete. Cleistogamous underwater flowers are present in many species (Duncan recorded them in populations of E. americana in Georgia). Chasmogamous flowers have small nectaries, but no report of insect visitors has been found. Self-pollination in E. hexandra, 2n = 72, is effected as the filaments elongate, bringing the anthers into contact with the stigmas (Hutchinson, 1955; Knuth). Self-pollination has been observed to occur in the same manner in plants of E. minima collected and grown indoors at the New York State Museum (collection from Stonington, Connecticut, G. C. & G. G. A. Tucker 3217 [NYS]). In the cleistogamous flowers of G. triandra, G0 = 40, and G1. hexandra the anthers are brought into contact with the stigmas as the filaments elongate. The pollen grains germinate in situ, and the tubes grow through the anther wall into the stigma (Frisendahl).

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